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The Origin of Angiosperms: New and Old Problems

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(1) psilophytes, which inspired the telome concept as a viable alternative to the now obsolete foliar theory; (2) seed ferns, which replaced ferns in the models of angiosperm origin; (3) bennettitaleans, which promoted the ranalean concept of a primitive angiosperm; and (4) caytonialeans, which can be used as an outgroup in phylogenetic analysis of angiosperm traits.

At present, palaeobotany is taking the lead in the development of a new paradigm. New fossil plants with angiospermoid characters have helped in formulating the pro-angiosperm concept2 (see below).

Studies of mid-Cretaceous flowers have shown what the primitive flowers were like2. Angiosperm entry into the fossil record has been documented by palynological analysis4. Due attention has been paid to the palaeoecology of early angiosperms5,6. These results have been augmented by painstaking morphological analysis of the supposedly primitive extant angiosperms5,6. In effect, the factual and conceptual bases of a new paradigm have been laid down, although a consensus has not yet been reached on many essential issues.

Morphological evolution

Because fossil plants are usually preserved as separated organs, palaeobotanical data are better suited for historical analysis of different traits than of whole-plant evolution. In addition, separate evolutionary histories of different organs are justified by the fact that organs in plants are less developmentally correlated than they are in animals.

In the following examples, the fossil record suggests some hitherto unconventional homologies between ancestral and descendant organs.

Leaf

The typical angiosperm leaf is broad with reticulate venation showing several orders of meshes. Superficially similar leaves occur in ferns, but here they grow by a marginal meristem while in angiosperms there are two kinds – marginal and plate meristems. Extant gymnosperm leaves are entirely different (except in Gnetum), but in the extinct gymnosperm groups of gigantopterids and peltasperms entire or lobed angiosperm-like leaves had evolved by parallel evolution from the fern-like precursors.

Fortunately, various evolutionary stages are preserved showing how the angiosperm leaf might have arisen. Initially, the original segmentation is evident in the entire blade because venation remains as it was in the ancestral bipinnate leaves. Obviously, the segments fuse marginally and the fusion meristem, while incorporated in the blade, still retains the marginal developmental program of not producing veins (which normally develop from submarginal initials). It is known, however, that fusion meristems readily change their developmental programs and even acquire new functions. Actually, more advanced stages of leaf fusion show reticulations in the zones of former fusion, suggesting that the fusion meristem evolved in the direction of what is now plate meristem in angiosperm leaves. Ultimate stages are not unlike the early angiosperm ‘disorganized’ reticulate venation (Fig. 11).

This example illustrates what may
be very typical for angiosperms: their superficially simple organs are condensed systems of ancestral organs (incidentally, leaves could be condensed fronds or leafy shoots) containing fusion meristems which made them developmentally plastic.

Flower
In a typical flower, the floral apex produces fertile organs - pistils and (or) stamens surrounded by sterile tepals. Some flowers, however, have sterile appendages - inner phyllomes - between stamens and pistils. These occur mostly in primitive magnoliids and hamamelids such as Liquidambar. Actually, such flowers are slightly modified dwarf shoots with fertile and sterile organs mixed in the apical zone, as in Ginkgo or Bennettitales. On the other hand, a fertile shoot of Irania, a Jurassic proangiosperm, can be reduced to a flower without inner phyllomes. Thus, in support of theoretical postulates by Meeuse, prototypes for at least two types of flower can be found among Mesozoic gymnosperms.

Stamen
Though traditionally seen as derived from microsporophylls, stamens (or at least some of them) show anatomical features of axial rather than foliar organs. Moreover, in some families there are fasciculate stamens arising from a common primordial knob. Their prototype could be a profusely branched sporangial system. Recently, a Cretaceous pollen organ was discovered that appears as an ideal prototype for a fasciculate stamen. It is an axis bearing lateral branches, some of which are sterile, while the others give off a pair of stalked subapical sporangial heads with a scaly sterile apex between them (Fig. 2). When their stalks are reduced, the sporangial heads appear not unlike the thecae of a typical angiosperm anther, with the sterile apex as a protruding connective. Thus, a stamen fascicle could be a condensed shoot of coaxial sporangial systems, with stamens - its lateral branching systems, and thecae - the ultimate branches.

Pollen
While monosulcate angiosperm pollen grains are obviously related to gymnosperm pollen of the same apertural type, the tricolpate and triporate grains that appeared slightly later are not readily derivable from any pre-existing pollen morphologies. A solution could be a derivation of the triaperturate type not from a single prototypical grain but from a permanent tetrad. Early Cretaceous tricolpate grains are similar to early monosulcates in exinal structure. Each lateral face of such tricolpates showing one of the colpi resembles the distal face of a monosulcate grain. Permanent tetrads occur in angiospermoid plant groups such as Himeriellaceae (Classopolis). Moreover, permanent tetrads with common ectoexine have been found in the Lower Cretaceous deposits. While this condition was achieved that early, it is conceivable that a final step in turning such tetrads into grains was made by pushing meiosis one cell cycle backwards.

Pistil
In the face of terminological confusion, it seems necessary to define pistils as gynoecial organs containing ovules and providing structures for extraovular pollination, while carpels are structural units of pistils. A pistil can be formed by one or several carpels, while a gynoecium consists of one to many pistils.

Current interpretations of carpels as involute, conduplicate or ascidiform macrosporophylls are remnants of the classical foliar theory created at the time when neither ontogeny nor relevant fos-
Fig. 3. Possible prototypes of pistils and stigmas. (a) Leptostrobus, showing bivalved cupules with stigmatic crests. (b) Caytonia, showing a globose cupule with a slit-like mouth covered with a vestigial supporting bract ('lip'). (c) Eoanthera, showing a four-valved gynoecium with a slit-like mouth covered with a vestigial supporting bract. (d) Baiia, showing a flask-like cupule with an apical 'corona'.

Box 2. Types of ovule

Orthotropous

Anatropous

by a fascicle of slender bracts — a possible precursor of a bushy stigma.

Thus, syncupuly — cupule fusion preceded syncarp, which appeared as early as the mid-Cretaceous as a second round of fusion, and there was more than one prototype of stigmas.

Double fertilization

Whether double fertilization is a unique character of angiosperms or whether it is shared with gnetophytes (and supposedly other proangiosperms of the same evolutionary grade) depends on the homology of the embryo sac nuclei. In angiosperms, double fertilization involves egg and polar nuclei while in Ephedra it is egg and ventral canal cell. However, the polar nuclei may correspond to gymnosperm eggs, while the angiosperm egg would be a sexualized ventral canal nucleus. The double fertilizations in Ephedra and angiosperms would then be strictly homologous.

To conclude, not a single angiosperm character is unique to the group. Absolute boundaries, cherished by typological thinking, just do not exist. Most typical angiosperm structures have obvious precursors (and sometimes more than one) among gymnosperms. As in the case of stigmas and double fertilization, the structures were ready; angiosperms had only to find a new function for them. When there is a structural gap, some radical restructuring can be suspected. More often than not it was a condensation of developmental processes. Multiple fusion meristems with their readily changeable genetic programs could in turn add to the structural plasticity of angiosperms.

Phylogeny

Phylogenetics seeks to reproduce historical relationships between taxa. Though much attention has been paid recently to the methods of constructing phylogenetic trees, phylogenetics depends primarily on ideas of homology (above) and actual chronology of evolutionary events as represented in the fossil record.

Among the early angiosperm records, flowers (though infrequent) provide phylogenetic information of primary importance, augmented by subordinate evidence from fruits, wood, leaves and pollen grains. Lower Cretaceous floral organs indicate lineages of chloranthoid, ranunculoid, paeonioid and platanoid affinities (Fig. 4). Most Lower Cretaceous leaves with cuticles are assignable to these groups, while a few more dicot and some unassigned monocot groups are suggested by leaf impression and pollen records.

In the late Albian and early Cenomanian, about 100-95 million years ago, angiosperms underwent explosive evolution, which produced inflorescences and single large flowers showing generalized magnolid, hamamelid and rosid characters. The dominant group — Normapolis, pollen-producing plants of diverse floral morphology — might comprise ancestral forms of the Myrales, Juglandales and Fagales.

Basic differentiation of the major angiosperm groups was thus accomplished. Such mid-Cretaceous forms as Asterocelastrus (Fig. 5), with a syncarpous ovary fused to a calyx cup, look quite modern and by conventional standards even more advanced than many extant rosids. Previously there was a tendency to lump the earliest chloranthoid, platanoid and paeonioid angiosperms with some later-appearing stocks. Systematists have now to reconsider their ideas of both the primitive-advanced character polarities and the basic taxon.

Strikingly, the mid-Cretaceous representatives of the major angiosperm stocks are morphologically less distant from each other than they are from their extant descendants. Floral organization could be initially more 'open' (plastic, capable of producing extreme variations). No transitional forms are known, however, between gyroecia with a single basal orthotropous ovule developing from the floral apex, as in Myrales, and carpels bearing several to many anatropous ovules. Moreover, similar differentiation existed among Mesozoic proangiosperms, gnetaleans and bennettitaleans with cupules containing a single basal orthotropous ovule on the one hand, and the caytonialean czekanowskialean plexus with cupules bearing many anatropous ovules on the other.
Among the early angiosperms, the 'orthotropous' group includes platanoid, chloranthoid, cypseloid and somewhat later-arising myriocoid forms, each of which can stem from different ancestors within the bennettitalean–gnetalean grade, while the 'anatropous' stock is represented by ranunculids, magnoliids, hamamelids and Cercidiphyllum-like trochodendroids. The anatropous group can be further subdivided into magnoliids–hamamelids with intrafloral phyllomes, and ranunculids–trochodendroids without them. While this distinction from both hamamelids and such trochodendrid group.

The Magnoliales but more convincingly assignable to the ranunculid–trochodendrid group.

Historical analysis thus provides a few distinctive characters that go back to the base of angiosperm phylogeny and even further down the proangiosperm level. They define lineages fairly distinct at the time of their first appearance, which hence were probably related to different groups of proangiosperms, as shown in Fig. 6.

Exact rooting of the basic angiosperm stocks can be accomplished after the remaining larger gaps in the fossil record (and the conceptual biases) have been removed. At present it appears that the long-neglected polyphyletic model is in the ascendant. It reconciles the Englerian and Hallierian concepts, which were seen as mutually exclusive for almost a century. It is for palaeoecology to explain why angiosperm characters appeared in more than one lineage.

Palaeoecology

Early angiosperms are almost universally conceived now as weedy r-strategists. However, the pre-Albian records are very rare, even though weedy plants tend to be abundant in the vicinity of the frequently flooded areas favourable for deposition of plant remains. During the Mesozoic era, such areas were occupied by horsetail (Equisetum) fern marshes, czekanowskias, swamp conifer forests and cycadophyte shrublands that extended into mesic ginkgo–conifer upland forests. Recent findings add gnetophytes as important components of both cycadophyte and czekanowskialean shrublands that occupied stream-side and seashore habitats.

In the beginning of the Cretaceous period, fern marshes were drastically reduced in northern hemisphere middle-latitude temperate–subtropical ecotonal areas such as Mongolia. They were replaced by some vanguard members of the shrubland cycadophyte–gnetophyte community. The first Neoecian angiosperm fossils appeared at this stage of ecological evolution.

The second mid-Cretaceous stage coincided with the rapid decline of czekanowskialaeans and bennettitaleans as dominant members of the middle-latitude shrubland communities. Immediately after that there was a steady increase in abundance and diversity of angiosperms.

Early angiosperm evolution may thus have been episodic, and closely linked with the history of certain gymnosperm communities. A notion of gymnosperms being out-competed by angiosperms is unlikely because angiosperms were far too rare before the bennettitalean extinction, which obviously correlated with the mid-Cretaceous environmental crisis. In disturbed environments, former dominants were replaced by some minor species in which condensed development was combined with more effective reproductive systems. Innovations included pollen with the exinal features of self-incompatibility syndrome and stigmas as counterparts of the same mechanism. Both features could develop from different gymnosperm precursory structures.

Lower Cretaceous angiosperms had small inconspicuous flowers clustered in spicate, racemose or globose inflorescences. They could be pollinated by wind, dipteran insects or both. Larger pollinators, such as beetles, might have preferred the sturdy flower-like cones of bennettitaleans. It is hardly a coincidence that single large flowers of many parts, resembling bennettitalean cones (hence rendered primitive), appeared soon after the extinction of bennettitaleans, which emptied the reproductive niche of beetle pollination.

The advent of comparatively small-leaved early angiosperms would have reduced total leaf mass, thus imposing dietary and related dental changes in dinosaurs. New groups with beaks and strong dental batteries, such as ceratopsids or hadrosaurs, were able to consume whole twigs with leaves and fruits. They in turn created a selective pressure in favour of endozoocorous seeds and fruits such as those recently found in coprolites.
To conclude, successive global environmental crises of the mid-Neocomian and Albain-Cenomanian times may have selected plants with condensed life histories capable of filling empty ecological niches. Each adaptive innovation appearing in a single lineage opened a new ecological niche, thus promoting similar innovations in other preadapted lineages. Evolutionary ‘fashions’, such as angiospermy, could arise in this way.

From what is now known of viral gene transfer mediated by fungi and bacteria, one can speculate that ‘horizontal’ spread of a new trait among coevolving lineages could be facilitated by this mechanism. Parallel evolution could be seen then as a joint effect of the ‘fashionmonger chase’ and non-sexual gene delivery. These hypotheses need now to be tested from palaeobotanical, morphological and genetic points of view.

References

In the next issue of TREE:
* Recruitment variability and the exploitation of marine populations, M. Fogarty et al.
* Phenotypic plasticity as a component of evolutionary change, J.D. Thompson
* Parasitism: a cryptic determinant of animal community structure, D. Mitchella and M. Scott
* Genetic control of migratory behaviour in birds, P. Berthold
* Ecology and evolution of long-lived semelparous plants, T. Young and C. Augspurger